

Regional growth decline of sugar maple (*Acer saccharum*) and its potential causes

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Abstract. Sugar maple (*Acer saccharum* Marsh) has experienced poor vigor, regeneration failure, and elevated mortality across much of its range, but there has been relatively little attention to its growth rates. Based on a well-replicated dendrochronological network of range-centered populations in the Adirondack Mountains (USA), which encompassed a wide gradient of soil fertility, we observed that the majority of sugar maple trees exhibited negative growth trends in the last several decades, regardless of age, diameter, or soil fertility. Such growth patterns were unexpected, given recent warming and increased moisture availability, as well as reduced acidic deposition, which should have favored growth. Mean basal area increment was greater on base-rich soils, but these stands also experienced sharp reductions in growth. Growth sensitivity of sugar maple to temperature and precipitation was non-stationary during the last century, with overall weaker relationships than expected. Given the favorable competitive status and age structure of the Adirondack sugar maple populations sampled, evidence of widespread growth reductions raises concern over this ecologically and economically important tree. Further study will be needed to establish whether growth declines of sugar maple are occurring more widely across its range.

Key words: *Acer saccharum*; acid rain; Adirondack Mountains; climate change; dendrochronology; northern hardwood forests; sugar maple; tree rings.

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INTRODUCTION

Sugar maple (*Acer saccharum* Marsh) is arguably the most ecologically and economically important species in the northern hardwood forests of eastern North America. Ecologically, sugar maple provides nutrient-rich litter to forest

soils (Long et al. 2009, Lucash et al. 2012), promotes N mineralization and reduces leaching of nitrate into groundwater (Lovett et al. 2004), and shapes the diversity of plant and animal communities (Beier et al. 2012a). Economically, the tree provides the raw materials for a profitable maple syrup industry, provides dura-

ble hardwood for furniture and flooring, and offers aesthetically pleasing fall foliage (Millers et al. 1989).

Unfortunately, the future of sugar maple in northern hardwood forests seems highly uncertain. Sugar maple suffers from a suite of ‘decline symptoms’—including branch dieback and foliar discoloration (Long et al. 1997, 2009), poor tissue nutrition (Hallett et al. 2006), regeneration failure (Sullivan et al. 2013) and elevated mortality (Horsley et al. 2000)—across central and northern portions of its range, including Pennsylvania (Horsley et al. 2000), New York (Sullivan et al. 2013), eastern Canada (Duchesne et al. 2002), and Vermont (Gavin et al. 2008). Collectively these symptoms have led some to define a ‘decline disease’ etiology for *A. saccharum* (Bauce and Allen 1991). Several proximate causes have been proposed, including soil acidification and nutrient depletion due to acid rain (Duchesne et al. 2002, Sullivan et al. 2013), insect outbreaks such as forest tent caterpillar (Welch 1963, Horsley et al. 2000), infection by *Armillaria* pathogens (Wargo and Harrington 1991), density-dependent competition (Bauce and Allen 1991), and climate-mediated stress and injury (Gavin et al. 2008, Hufkens et al. 2012). Decline symptoms have been more severe (or evident) in populations where the co-occurrence of two or more of these stressors has been documented (Driscoll et al. 2003).

Among the larger-scale stressors of sugar maple, acid rain and climate change may pose the greatest historical and future threats to the species across its range. Sugar maple is calciphilic and therefore is vulnerable to effects of acidic deposition in poorly buffered soils, including loss of soil calcium (Ca) and the mobilization of inorganic aluminum (Al), which is toxic and inhibits root uptake of Ca and other nutrients (Lawrence et al. 1995, Cronan and Grigal 1995). Recruitment, vigor, crown condition and foliar nutrition of *A. saccharum* tend to be lower on base-poor soils, relative to base-rich soils (Hallett et al. 2006, Sullivan et al. 2013).

With respect to climate change, niche models (Iverson et al. 2008) indicate that sugar maple will experience one of the largest reductions in range and importance among eastern deciduous trees under a range of projected climate scenarios. To date, however, there has been relatively

little investigation of climate sensitivity in extant *A. saccharum* populations. Gavin et al. (2008) observed mostly weak and non-stationary (changing over time) climate-growth relationships for two populations in Vermont during the last several decades. Climate-mediated injury may also play a role, such as defoliation due to an early thaw—late frost event that affected an area of over 8700 km² across New England in 2010 (Hufkens et al. 2012).

Compared to the visible symptoms of decline, relatively little attention has been given to the long-term patterns of sugar maple growth rates (Kolb and McCormick 1993, Gavin et al. 2008), despite the fact that growth and yield have more direct implications for both the ecological and economic value of the species. Decreasing growth rates have been used as a proxy of tree vitality and susceptibility, and in many species have been observed as a precursor to mortality when coupled with additional stressors (Pedersen 1998, Suarez et al. 2004). Changes in tree growth can also provide a long-term empirical basis to draw inferences about causal factors associated with decline etiology, which often involve a complex set of precursors and proximate stressors. Few studies of *A. saccharum* have documented whether declining health and vigor are associated with declining growth (Long et al. 2009), or if visibly healthy stands are experiencing changes in growth that may be consistent with ‘niche model’ predictions in a changing climate.

In this study, we assessed growth rates of range-centered sugar maple populations using a well-replicated sampling network that included both healthy and unhealthy populations across the Adirondack Mountains (USA). Our sampling network captured a wide range in soil chemistry—from well-buffered and nutrient rich to heavily acidified and nutrient poor—in a recently warming portion of the species range (Beier et al. 2012b). The health, vigor, and recruitment of *A. saccharum* are much lower in culturally acidified Adirondack forests, but due to variations in surficial geology, there exist areas of highly-buffered base-rich soils that support visibly healthy populations (Sullivan et al. 2013). We compared recent *A. saccharum* growth rates and trends across sites varying in soil chemistry (and visible indices of health and vigor) and evaluated

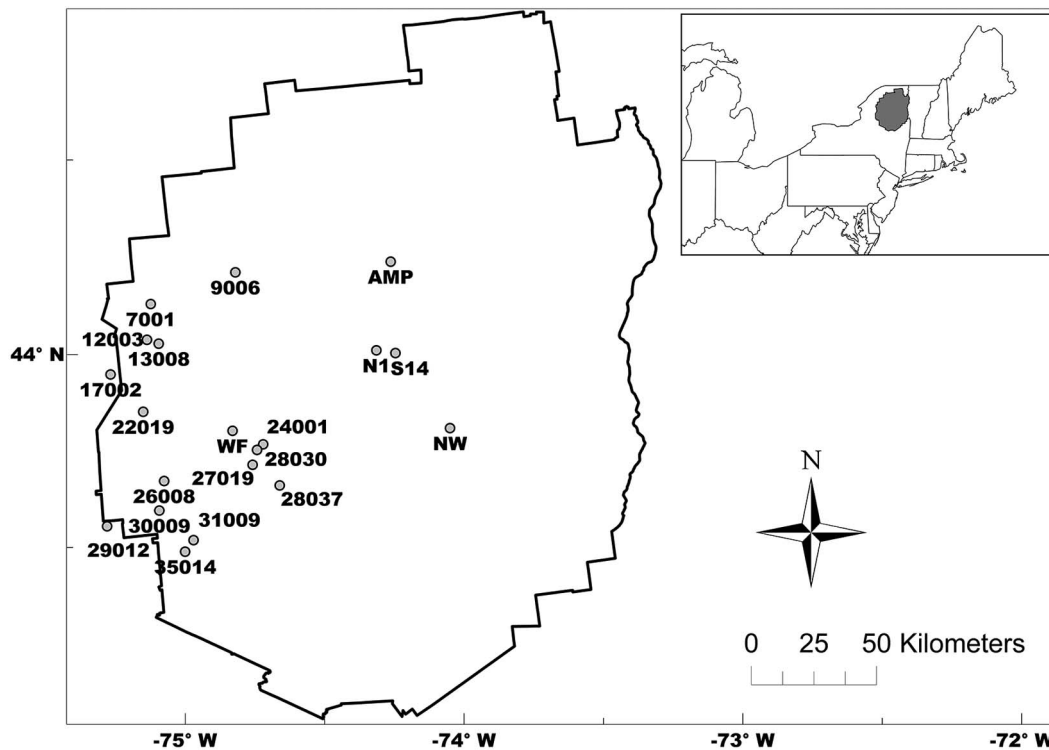


Fig. 1. Network of study sites ($n = 18$) across the Adirondack Mountains of New York State, USA.

the sensitivity of growth chronologies to recent climatic variability. We expected to observe lower absolute growth rates (measured as basal area increment) on acidified soils with low base saturation and high exchangeable [Al], relative to well-buffered, nutrient-rich soils. No population-wide growth trends were expected, given the age and competitive status of the trees sampled; however, we hypothesized that trees on poor soils would exhibit less overall variability in growth due to nutrient limitation. Lastly, as a cold-temperate species with deterministic growth behavior (Bauce and Allen 1991), we expected *A. saccharum* growth to exhibit a positive sensitivity to temperature and precipitation during the growing seasons both prior to and during the year of ring formation, although these climate-growth relationships may have been variable over time (Gavin et al. 2008).

METHODS

Selection of study sites

We sampled 18 *A. saccharum* populations in a

network of upland hardwood forests distributed across the western and central Adirondack Mountains (Fig. 1). Sites were originally established as part of the Western Adirondack Stream Study (Lawrence et al. 2008) and were selected by Sullivan et al. (2013) to capture a regional gradient of soil base availability, which is known to shape *A. saccharum* nutrition and health (Long et al. 2009, Sullivan et al. 2013). Soil samples from Oe, Oa, A, and B horizons were assayed for exchangeable Ca, Mg, Al, and base saturation (see Sullivan et al. 2013 for methodology).

Growth measurements and tree-ring chronologies

Acer saccharum growth was measured through two tree-ring sampling efforts using our site network. In 2009, increment cores (2 per tree) were collected at each site from 6–9 dominant or co-dominant *A. saccharum* trees with a diameter at breast height (DBH; 1.3 m) ≥ 35 cm. To improve stand-level replication, we cored an additional 4–10 trees per site in 2012, using a lower minimum DBH of 30 cm. Using this threshold, most, if not all, canopy-dominant or

co-dominant *A. saccharum* trees were sampled in every plot; DBH and crown position were recorded for each tree. Increment cores were measured to 0.001 mm accuracy with a sliding stage laser micrometer (Velmex Corporation, Bloomfield, New York, USA). Program COFECHA was used to verify visually cross-dated series of radial increment as well as identify measurement errors, false rings, and missing rings. Two pairs of nearby sites with similar soil chemistry and land use history were combined (31009 with 35014; 12003 with 13008) to remedy small sample sizes.

The sample population consisted of 18 sites, 242 trees, and 450 ring-width series. Using these raw ring widths, we compiled two data sets for analysis: (1) basal area increment (BAI) at the individual tree, site (average), and regional population (average) levels; and (2) ring width indices (RWI) derived from detrended and standardized chronologies using ARSTAN (Cook 1985). The BAI time series data were used to assess trends in *A. saccharum* growth, because the BAI calculation accounts for geometric bias in raw ring width series. Average site-level BAI during 1970–2008, selected to represent a period most temporally relevant to our soils data, at the site level was used to compare absolute growth rates among sites, and to estimate correlations between soil chemistry and increment growth. The RWI series—based on detrended and standardized chronologies derived from the same raw data as BAI—was used to assess the climate sensitivity of *A. saccharum* growth at the site level during 1909–2008.

Growth trends

We calculated basal area increment (BAI) for individual trees using the `bai.out` function in the `dplR` package (Bunn 2008). Mean BAI estimates were summarized by site ($n = 18$) and the entire regional population (all trees; $n = 242$), and by quartiles of the pooled size class distribution (based on DBH) to evaluate growth patterns across different size classes.

We used a multiple-step approach to assess temporal changes in growth based on the sugar maple BAI data. First, a segmented regression technique was used to identify shifts in the BAI time series for each individual tree. When a shift was identified, we then assessed whether the BAI

time series after the shift experienced a positive trend, negative trend, or random walk. The start years of trend calculation were based on the “breakpoint” identified from the analysis, which was found by minimizing the residual sum of squares in a segmented linear regression fit (Zeileis et al. 2003). To assess trends, we used a two-part non-parametric procedure that provides comparable outputs to a least-squares regression, but is more robust to outliers. First, the Mann-Kendall test was used to evaluate directionality in the time series; a significant τ statistic ($p < 0.05$) indicates that a time series is consistently moving upward or downward and is not a random walk (Kendall 1938). Next, the non-parametric Theil-Sen slope (Sen 1968) was calculated to estimate a linear rate of change ($\text{mm}^2 \text{decade}^{-1}$) in a time series. Relative to least-squares regression, the Theil-Sen method greatly reduces the effect of outliers on low-frequency trend estimation (Sen 1968), which is preferable given the high interannual variability of tree-ring data.

To summarize, each tree's BAI time series was fitted with a segmented regression, the breakpoint was identified (if one existed), and the Mann-Kendall tau and Theil-Sen slope for the period following each breakpoint were calculated. The tau statistic and slope were used to assess directionality (significance) and magnitude ($\text{mm}^2 \text{decade}^{-1}$), respectively, of the growth patterns over time. The timing (calendar year) of the breakpoint was also recorded for each tree.

Soil chemistry

To test the hypothesis that soil chemistry influences *A. saccharum* growth, Pearson correlations were evaluated between site-level soil chemistry (exchangeable Ca, exchangeable Al, and base saturation) and three growth parameters: mean site-level BAI (1970–2008), the timing of the BAI “breakpoint” (growth shift), and the growth trend magnitude (rate) following the “breakpoint.” Exchangeable Mg was correlated with Ca across all soil horizons ($p < 0.01$) and subsequently removed to avoid collinearity among soil chemistry variables.

Climate sensitivity

Standardized chronologies were created using ARSTAN (Cook 1985) to generate ring width

indices (RWI) for climate analysis. Geometric trends and effects of disturbance were reduced through two rounds of detrending: (1) a negative exponential curve or linear regression (best fit) to account for geometric bias (Cook 1985), and (2) a data-adaptive smoothing spline (Friedman 1984) for disturbance and release events. Releases were identified based on the Lorimer and Frelich (1989) classification system. Following Pederson et al. (2004), chronologies that did not exhibit releases were fit with a horizontal line. Detrending's primary purpose is to separate the geometric and ecological noise from the climatic signal (Fritts 1976, Cook and Kairiukstis 1990), developing dimensionless and standardized chronology tree-ring indices for comparison with climate. After detrending, series were grouped by site and averaged annually using a robust biweight mean to create site-level ARSTAN chronologies (Cook and Kairiukstis 1990). Site-level ARSTAN chronologies were also aggregated into a regional composite using the first principal component (PC1) from a principal components analysis of all site-level ring-width indices (RWI).

To represent local climate conditions across the site network, we used 4 km resolution gridded historical estimates of monthly temperature (Tmax and Tmin) and precipitation (PPT) provided by PRISM (PRISM Group, Oregon State University, Corvallis, Oregon, USA; <http://www.prism.oregonstate.edu>). Variables included monthly Tmax, Tmin, and PPT for the same year of growth (t) and prior year ($t - 1$). Data extracted from PRISM cells associated with study sites were averaged to produce a shared climatology for the regional population, and to account for uncertainty associated with PRISM temperature estimates in this region (Beier et al. 2012b, Bishop and Beier 2013). To evaluate drought, monthly Palmer Drought Severity Index (PDSI) was collected from the National Climatic Data Center's online database for New York State, Northeastern Plains division (www.ncdc.noaa.gov/; Diamond et al. 2013). We focused on 1909–2008 for climate-growth analyses due to issues with data reliability and continuity.

Climate sensitivity of the RWI (standardized chronologies) for the study period (1909–2008) was evaluated using a seasonal moving window correlation screening procedure. Pearson correla-

tion coefficients between the site-level RWI and 3-month seasonal climate windows with a 1-month time step from January to March of the previous year of ring formation through July–September of the year of ring formation, following a similar approach by Liu et al. (2013). Only correlations significant at $p < 0.05$ were considered further. The same analysis was conducted with the regional composite RWI using the first principal component (PC1), which explained 47.3% of the variance in all site-level RWI series.

To account for temporal variability in climate sensitivity, we used time varying parameter (TVP) regression modeling based on a state-space model using the Kalman filter (Kalman 1960). The TVP method is a commonly used approach that allows for a time-dependent relationship between ring-width indices and climate (Cook and Johnson 1989, Visser et al. 2010), and the Kalman filter improves signal-to-noise ratio by introducing a noise term to the TVP model that allows for dynamic RWI responses to climate. TVP regressions were analyzed only for those seasonal climate variables correlated with RWI, based on the screening described above. In lieu of building TVPs for each site, we analyzed the regional composite 'signal' based on first principal component (PC1), as above. Prior to model fitting, climate data were standardized (zero mean, standard deviation of 1), and PDSI was pre-whitened to reduce built-in autoregressive persistence.

Except for COFECHA and ARSTAN, all analyses were conducted in R (R Development Team 2010) with the *zyp* (Bronaugh and Werner 2009), *dplR* (Bunn 2008), *vegan* (Oksanen et al. 2011), *strucchange* (Zeileis et al. 2002), and *dlm* (Petris 2010) packages.

RESULTS

Growth trends

Decreasing growth was observed after 1970, with intensification after 1990, in the majority of *Acer saccharum* trees sampled across the Adirondack Mountains (Fig. 2A; Appendix: Fig. A1). A segmented regression model fit to mean population BAI ($n = 242$ trees; 1909–2008) indicated a significant shift to a negative growth trend occurred in 1970, followed by a second shift after 1990 (based on the first and second

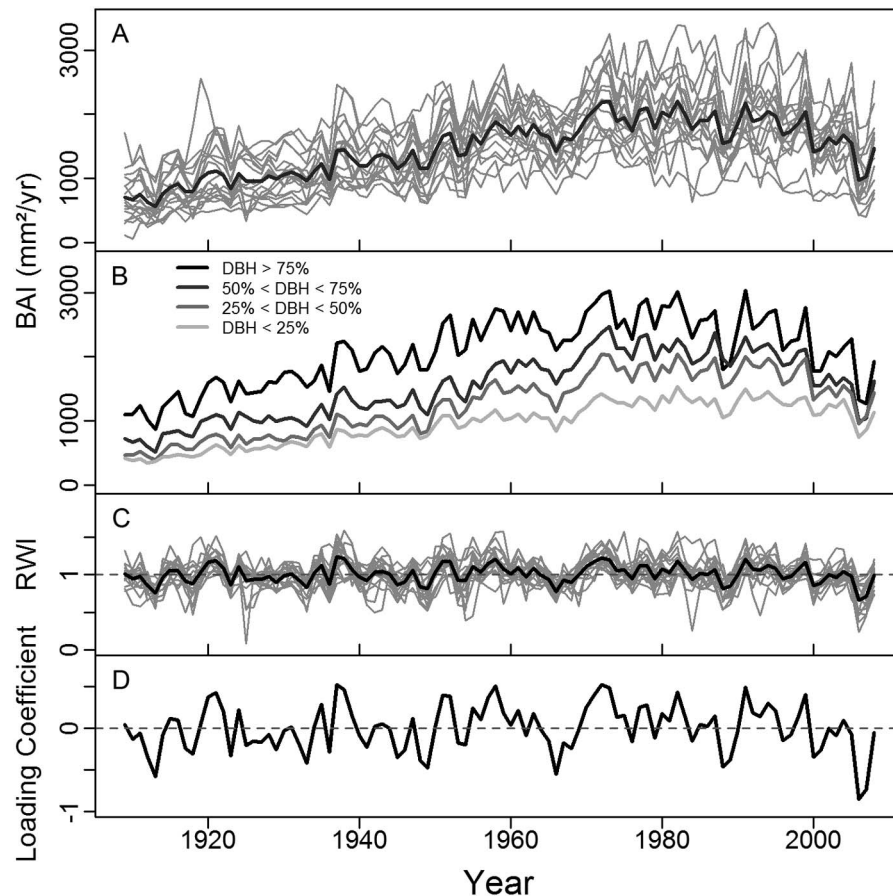


Fig. 2. Growth patterns of canopy-dominant *Acer saccharum* across a network of upland forests ($n = 18$) in the Adirondack Mountains, New York (USA). Plots include (A) basal area increments (BAI) averaged by site (grey lines), (B) BAI averaged by quartiles of the pooled size distribution (Diameter at Breast Height; DBH), (C) ARSTAN chronologies for each site (grey line) and averaged across the region (black line), and (D) composite chronology derived from principal component analysis (PCA) of ARSTAN chronologies from 1909–2008.

“breakpoints”). Mean BAI exhibited negative trends across diameter classes (quartiles) after 1970, although trees in the smallest size class (lowest DBH quartile) exhibited the smallest trend magnitude (Fig. 2B).

We note that creation of ARSTAN chronologies (Fig. 2C; Appendix: Fig. A2) removed many of these growth trends, as purposed to evaluate radial growth sensitivity to high-frequency variability in climate. The first principal component (PC1), derived from the PCA of all 18 ARSTAN site chronologies, accounted for 41.1% of variance (Fig. 2D).

Of the 242 trees sampled, we found that 139 trees (57%) exhibited negative growth trends ($p < 0.05$) after the most recent “breakpoint” in

segmented regression fits (Table 1). In contrast, only 13 trees (5%) exhibited positive growth trends ($p < 0.05$), and the remaining 90 trees exhibited a ‘random walk’ pattern based on Mann-Kendall tests ($p > 0.05$; Fig. 3). Frequencies of growth trends are listed in Appendix: Table A1 over varying confidence levels.

Of the 289 breakpoints calculated after 1970, 140 (48%) were followed by negative growth trends ($p < 0.05$), 33 (12%) were followed by positive growth trends, and the remaining 116 exhibited a random walk (Fig. 3). At the site level (mean BAI by site), 13 of the 18 populations (72%) exhibited significantly negative BAI trends after the most recent growth shift. Growth trend estimates at the individual and site levels were

Table 1. Summary of growth trends and demographic parameters for sample populations of sugar maple (*Acer saccharum*) in the Adirondack Mountains, New York, USA.

Sites	<i>n</i>	Last breakpoint	Negative growth	BAI trend	Mean age	Mean DBH
S14	10	1993	7 (70)	−441.9	153.3	46.1
12003/13008	15	1992	13 (87)	−1400.5	86.6	44.5
9006	12	1990	7 (58)	−525.4	96	44.1
28030	14	1990	9 (64)	−407.9	145.7	47.2
NW	14	1990	4 (29)	−215.8	101	41.8
22019	13	1989	11 (85)	−760.1	99.2	43.3
N1	15	1989	5 (33)	−277	117.1	47.5
29012	15	1983	9 (60)	−193.9	90.2	42.5
WF	14	1983	4 (29)	−134.3	123.5	48.3
28037	14	1982	10 (71)	−521	119.2	40.2
17002	14	1980	8 (57)	−658	87.4	41.1
26008	12	1978	7 (58)	−99.2	96.5	37.3
7001	14	1971	11 (79)	−325.4	92.5	48.3
30009	15	1971	9 (60)	15	116.7	41.9
24001	10	1970	5 (50)	−369.2	113.4	47.7
31009/35014	16	1970	10 (63)	−323	102.9	42.8
AMP	11	1957	6 (55)	−200.8	176.5	53.5
27019	14	1946	4 (29)	81.6	84.6	37.7
Stand	242	1990	139 (57)	−423.2	107.9	44.1

Note: Columns include sample size (*n*), year of last breakpoint in the BAI (basal area increment) time series (average by site) using segmented regression, number (with percentage in parentheses) of trees with significant negative growth trends based on Mann-Kendall tau ($p < 0.05$), estimated mean rate of change in BAI since last breakpoint ($\text{mm}^2 \text{decade}^{-1}$), mean age in 2009, and mean DBH (cm).

not associated with age or size (DBH) parameters ($p \gg 0.05$; Fig. 4).

Soil chemistry

Sugar maple trees on base-rich soils had higher growth rates than trees on moderate or base-poor soils. Mean growth increment from 1970–2008 was negatively correlated with exchangeable $[\text{Al}^{3+}]$ (-0.51 , $p < 0.05$), and was positively correlated with base saturation (0.41 ; $p = 0.09$) and exchangeable $[\text{Ca}^{2+}]$ (0.42 , $p = 0.08$), in the A horizon (Appendix: Table A2). Site-averaged A horizon soil chemistry values are summarized in Appendix: Table A3.

We found no association between soil chemistry and growth trends; neither the direction (Mann-Kendall tau) nor the magnitudes (Theil-Sen slope) of recent BAI trends ($p \gg 0.05$) of *A. saccharum* were associated with soil variables at the site level. Populations on base-rich soils experienced declining growth at similar rates as those on moderate and base-poor soils.

Climate sensitivity

Sugar maple growth sensitivity to climate was variable across sites and over the 1909–2008 period. The first principal component of the regional chronology (PC1) was negatively correlated ($p < 0.05$) with July–September TMax,

June–August TMin, and July–September TMin of the prior year ($t - 1$); and positively correlated with February–April PPT of the prior year ($t - 1$) and June–August PPT of the same year (t ; Fig. 5). Neither the regional chronology (PC1) nor the site-level chronologies were associated ($p > 0.05$) with monthly PDSI over the 1909–2008 period.

Growth sensitivity to these climatic factors was non-stationary in several cases. We observed the following shifts in *A. saccharum* growth responses to climate: (1) prior year ($t - 1$) February–April PPT shifted from a null effect to a positive effect on growth (Fig. 6A); (2) same year (t) June–August PPT steadily changed from a positive to a null effect in recent decades (Fig. 6B); and (3) prior year ($t - 1$) July–September TMin shifted from a null to a negative effect over recent years (Fig. 6C). Although the chronologies were not correlated with monthly PDSI, prior year ($t - 1$) PDSI from May through September had a positive effect on growth during the 1960s drought, followed by a decreasing to null effect during and after the 1970s pluvial.

DISCUSSION

Growth rates of sugar maple—a keystone species in the northern hardwood forests of eastern North America—have been unexpectedly

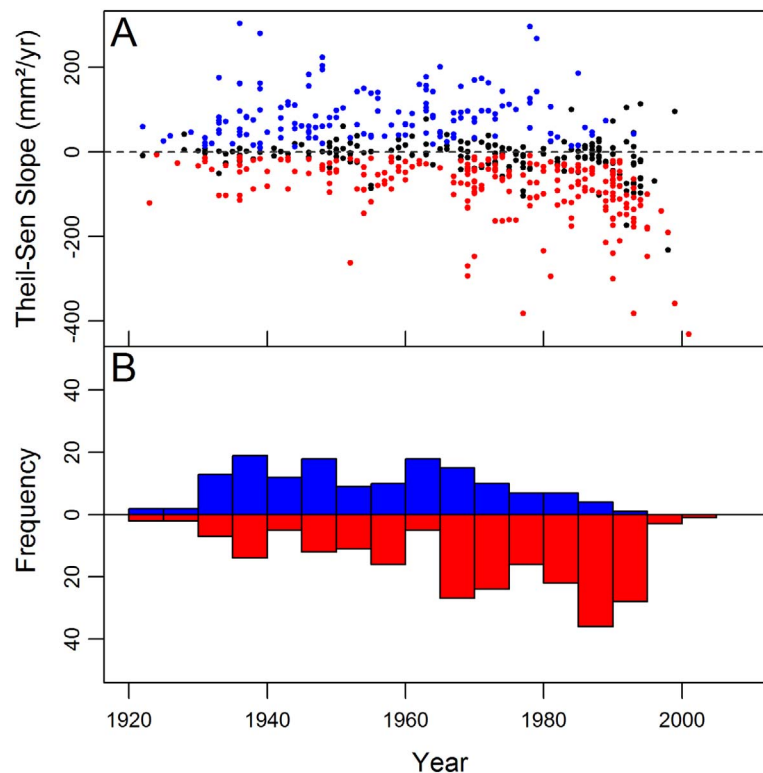


Fig. 3. Breakpoints in segmented regression model fits for all sampled *Acer saccharum* trees ($n = 242$). Segmented regressions were fit to each individual tree BAI (basal area increment) time-series, with (A) breakpoint year (x -axis) plotted against the Theil-Sen slope coefficient (y -axis) estimated for the period following the break and (B) a histogram for the distribution of breakpoint occurrences in time that are followed by a significant trend ($p < 0.05$). Breakpoints preceding positive slopes are shown in blue and negative slopes are in red. Significant trends (Mann-Kendall tau, $p < 0.05$) in top plot are colored in blue and red for positive and negative slopes, respectively; black points have no significant trends following the breakpoint.

decreasing in recent decades in range-centered populations across the Adirondack Mountains. The observed shifts to negative trends in growth were unexpected given the competitive status and the relatively young ages of these long-lived trees. Similar growth patterns were observed across tree age and size distributions, indicating that the decreasing growth rates were not a result of old age or large diameter. Although acidic deposition has decreased and climate has become more favorable for sugar maple growth, we observed predominantly declining patterns of growth across the Adirondack region. The discovery of these declining growth rates, evaluated with the known lack of sugar maple regeneration on less fertile soils (Sullivan et al. 2013), identifies a major concern for this ecolog-

ically and economically important tree species.

Adirondack sugar maple trees on base-rich soils have higher growth rates than trees on naturally base-poor and culturally acidified soils (based on basal area increment; Sullivan et al. 2013; this study). Depletion of Ca and mobilization of Al in soils resulting from acidic deposition is well documented within the Adirondack region (Lawrence et al. 1995, Sullivan et al. 2006, Johnson et al. 2008) and elsewhere (Likens et al. 1996, Bailey et al. 2005). The negative effects of Ca depletion and Al mobilization on the health and regeneration of *A. saccharum* are also well documented (Duchesne et al. 2002, Long et al. 2009, Sullivan et al. 2013), as are the positive effects of adding calcium to stressed *A. saccharum* stands (Long et al. 1997). These effects are most

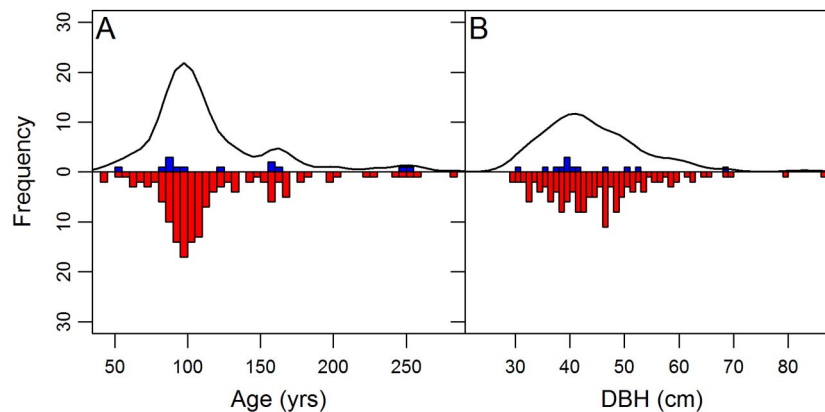


Fig. 4. Distribution of growth trends across (A) age classes and (B) size classes in the *Acer saccharum* sample population. Histograms depict frequency of significant positive (blue) and significant negative (red) trends for individual trees, based on the growth pattern following the most recent breakpoint (from segmented regression model fitting). Smoothed kernel density function (black line) for total number of trees illustrates sample depth distribution.

pronounced on naturally acidic, poorly-buffered soils on granitic parent materials, which are prevalent in the Adirondack Mountains (Driscoll et al. 2001), while irregular ‘patches’ of base-rich and highly-buffered soils are much less vulnerable to acidification (Page and Mitchell 2008, Beier et al. 2012a). Our results confirmed the positive effects of Ca availability, and negative effects of soil Al mobilization, on the above-ground productivity of *A. saccharum* trees.

Our data shows, however, most sugar maple trees in the Adirondacks have declining growth rates over the past several decades and that these trends were consistent regardless of soil Ca or Al availability. This regional-scale decrease has been most evident since the amendments to the Clean Air Act in 1990—a period during which we have high confidence that all of the trees sampled were canopy-dominant. Given significant reductions in acid deposition in the Adirondacks and surrounding regions since the 1990s (Lawrence et al. 2012), we expected positive growth trends to have occurred via recovery of the slow-growing trees (and stands) on acid-impaired sites. In other words, with the amelioration of a known stressor that exacerbates a limiting factor (soil Ca availability), *A. saccharum* growth on poor sites should have increased and begun to approach higher rates of growth observed on higher quality sites. Yet the lack of recovery of *A. saccharum* growth on acid-impaired sites is

consistent with a recent study that found no evidence of soil recovery—in terms of base saturation or Al mobilization—in the Adirondacks following reductions in N and S deposition since 1990 (Lawrence et al. 2012). Further study is needed to understand how temporal changes in soil nutrition due to acidic deposition could differentially shape sugar maple growth on base-rich versus base-poor soils in the Adirondacks and elsewhere across its range.

Niche model projections under climate change scenarios suggest a drastic reduction in the future range, distribution, and importance of sugar maple in eastern US forests (Iverson et al. 2008). We did not detect any consistent patterns of climate sensitivity in range-centered *A. saccharum* that would indicate recent warming was associated with the recent downward trajectory in its growth. Growing season precipitation in the Adirondacks has increased or remained steady during the period of sugar maple growth decline (Appendix: Fig. A4) with synchronous increases in minimum temperatures and lengthening of growing seasons (Hayhoe et al. 2008, Beier et al. 2012b; Appendix: Fig. A3). Moreover, during the last two decades, the northeastern US has experienced one of the wettest periods of the last 100–500 years (Pederson et al. 2013). Given these changes in regional climate, we might have expected to observe increases in forest productivity (Boisvenue and Running 2006), but our

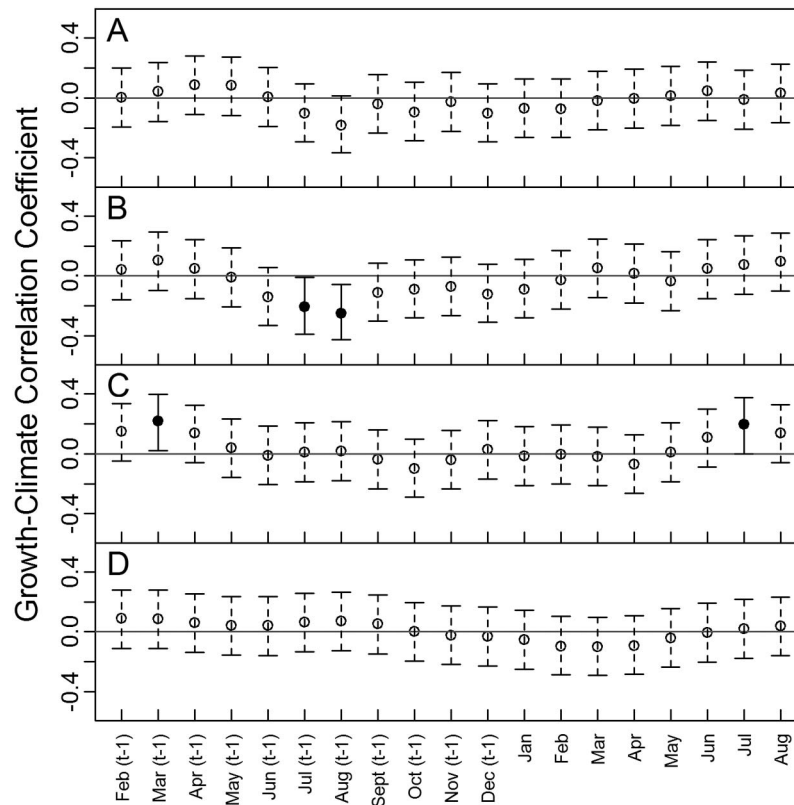


Fig. 5. Summary of *Acer saccharum* growth sensitivity to climate. Correlations (circles) between composite chronology and monthly climate variables over 1909–2008 for (A) maximum temperature, (B) minimum temperature, (C) precipitation, and (D) Palmer's Drought Severity Index (PDSI). Each climate variable is calculated using a 3-month moving window with a 1-month time step, beginning with January–March of prior year and ending with July–September of current year. Climate variables are identified by the central month of 3-month window on the x -axis (e.g., Feb includes January–February–March). 95% confidence intervals represented by error bars. Significant correlation coefficients ($p < 0.05$) are represented by solid circles.

data clearly indicate otherwise—only a small minority of sugar maple trees have increased their growth rates during this time.

Growth chronologies of range-centered *A. saccharum* populations in the Adirondacks exhibited a relatively weak but non-stationary sensitivity to climatic conditions. Non-stationarity in growth-climate relationships, which suggests that *A. saccharum* populations are responding differently to climate variability today relative to the mid-20th century, was also observed in Vermont (Gavin et al. 2008), and partly explains the weak correlations between climate and *A. saccharum* chronologies during the study period (1909–2008). We did observe a growth sensitivity of *A. saccharum* to the well-documented drought

of the 1960s in the northeastern US, but we also observed a clear pattern of BAI recovery post-drought and a lack of sensitivity to drought severity (PDSI) since 1970. These insights, along with recent increases in moisture availability suggest that sugar maple growth decline is unrelated to moisture limitation.

Because we sampled only canopy dominant or co-dominant trees, there is the possibility that a “big-tree selection bias” could influence our results. New research suggests that a collection dominated by large diameter trees typically is associated with a moderate to large increase in growth rates in which more carbon is fixed in recent decades (Brienen et al. 2012, Stephenson et al. 2014). Our observations of sharply reduced

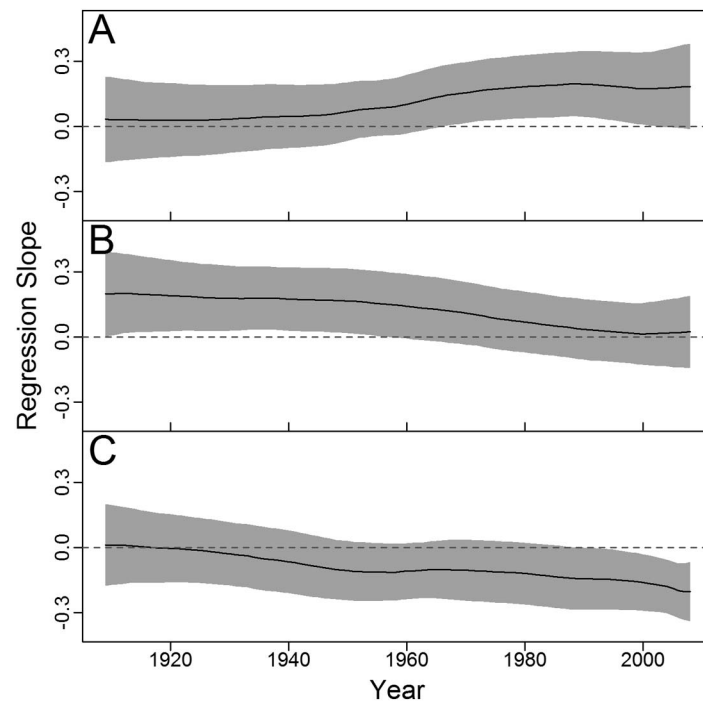


Fig. 6. Non-stationarity in *Acer saccharum* growth sensitivity to climate. Time varying parameter (TVP) regression slope coefficients (black lines) plotted over time (1909–2008) for (A) prior year February–April precipitation, (B) same year June–August precipitation, and (C) prior year July–September TMin. The grey shaded area illustrates the 95% confidence interval. Regressions were built with the composite chronology as the response variable and regional mean climatic variables as predictors.

growth rates in canopy dominant *A. saccharum* populations across size classes are in strong contrast with this expectation. The negative trends and estimated absolute changes in BAI since 1970 suggest that the net productivity of Adirondack sugar maple populations is in decline.

In conclusion, given the high ecological and economic importance of sugar maple in northern forests, new evidence of its decreasing growth and productivity—including areas where soils remain base-rich and populations indicate no outward signs of stress or decline—warrants significant concern. Long et al. (2009) suggest that similar patterns may be found in sugar maple populations across the US Northeast, and while our study strongly supports this hypothesis in a region covering a large portion of the over 8,000 km² Adirondack Park, further study of long-term growth patterns and their associated factors is needed. Reductions in growth alone do not necessarily indicate that a population is in

decline, but may be a precursor of increased mortality and/or decreased recruitment, which often emerge as part of a decline complex (Manion 1981). Decreased recruitment has already been observed in our study region on relatively acidified soils (Sullivan et al. 2013). Among numerous potential inciting factors for sugar maple, insect defoliator outbreaks (e.g., forest tent caterpillar; Gross 1991) and freeze-thaw injuries (Hufkens et al. 2012) may be most prevalent. In addition, from an applied perspective, while visual cues of defoliation and branch dieback are useful indicators of tree health, changes in growth rates are more directly relevant for forest management decision-making, as well as ecosystem services such as syrup production, carbon sequestration, habitat provision and nutrient cycling. As we observed, visibly ‘healthy’ sugar maple populations can be experiencing downward shifts in growth rates that may prove to be problematic. Further study is needed to establish whether growth declines of

sugar maple are occurring more widely across its range, and if so, to address the sustainability of this iconic and highly valued species of the northern hardwood forest.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES15-00260.1.sm>